Hydrobiologia 384: 101–110, 1998.

The limnology of Lake Torrens, an episodic salt lake of central Australia, with particular reference to unique events in 1989

W. D. Williams[1], P. De Deckker[2] & R. J. Shiel[3]
[1] *Department of Zoology, University of Adelaide, Adelaide, SA 5005, Australia*
[2] *Department of Geology, Australian National University, Canberra, ACT 2601, Australia*
[3] *Murray-Darling Freshwater Research Centre, Albury, NSW 2640, Australia*

Key words: salt lakes, desert lakes, Lake Torrens, Australia, episodic

Abstract

Lake Torrens, a large (~ 6 000 km^2), episodic, saline playa lake in arid central Australia, filled for the first recorded time in March 1989. This unique event followed unprecedently heavy rain over its catchment. Water remained in the lake until early 1990. Salinities remained low (< 40 g l^{-1}) until November 1989, then increased rapidly to > 200 g l^{-1} before the water evaporated completely. Na and Cl probably dominated the ions. Twenty-nine taxa of aquatic animals were recorded. Crustaceans dominated and of these *Parartemia minuta* (anostracan), *Daphniopsis queenslandensis* and *Moina baylyi* (cladocerans), and several species of ostracods were the most important. Other significant taxa included *Tanytarsus barbitarsis* (chironomid), *Brachionus plicatilis* (rotifer) and *Craterocephalus eyresii* (fish). The fauna was dominated by widespread forms that are either part of a distinct assemblage found widely in central Australian salt lakes (especially *P. minuta, D. queenslandensis, M. baylyi* and *Trigonocypris subglobusus* [ostracod]), or cosmopolitan forms (*B. plicatilis*), or forms found widely in Australian salt lakes (e.g. *Diacypris compacta, Tanytarsus barbitarsis*). However, possibly three new species also occurred: a new species of a new genus of mytilocypridinid, *Branchinella* nov.sp. and *Heterocypris* nov. sp. Their occurrence is anomolous. It is suggested that further work will show that they too are widely distributed. Both genera of the latter two taxa are typical of temporary waters and specimens may have been washed in from nearby water-bodies.

Sixty-four species of bird were recorded when the lake contained water, many breeding. The breeding of the banded stilt (*Cladorhynchus leucocephalus*) was notable; breeding of this species had been unknown in South Australia since 1930. A large population built up until breeding was stopped by predation from the silver gull (*Larus novaehollandiae*). When dry, the lake has a depauperate but well-defined and regionally restricted 'terrestrial' fauna (scorpions, spiders, beetles, ants).

Introduction

Almost 20 per cent of the world's land surface comprises arid and hyper-arid regions, i.e. regions receiving < 300 mm mean annual precipitation. Notwithstanding their aridity, numerous lakes occur in such regions: for 'deserts', a climatic category approximately equivalent to arid and hyper-arid regions, Meybeck (1995, Table 11) listed almost 1000 lakes with surface area > 1 km^2, with a total lake area > 125 000 km^2 (of which, however, some 50 per cent is contributed by the Aral Sea in central Asia). Meybeck's values are likely to be underestimates because many usually dry lakes in deserts would undoubtedly have been excluded from consideration. Lakes that are usually dry, nevertheless, may on occasion contain substantial amounts of water. These occasions occur more or less unpredictably, often infrequently, and the lakes they fill are best referred to as *episodic* lakes (*sensu* Williams, in press). They are confined to arid and hyper-arid regions, but are most typical of arid regions.

Episodic lakes *ipso facto* have been little studied by limnologists. They are often inaccessible, only infrequently and unpredictably contain water as noted, and many if not most are saline when water is present. These features, however, do not mean that they lack scientific interest or biological value; they are simply difficult to study with few opportunities to do so. They are best known in Australia. Here, recent limnological studies include those of Bayly (1976), Williams & Kokkinn (1988) and Williams (1990) on Lake Eyre, and Timms (1993, in press a, b) on the Paroo lakes of inland New South Wales and Lake Wyara, Queensland.

An opportunity to study another Australian episodic lake occurred in 1989 following unprecedently heavy rain in March of that year over the catchment of Lake Torrens, a lake not known to have filled in recent times. The main aim of the present paper is to report on this unique event and its results. A second aim is to summarize other limnological features of the lake which despite its large area (it is the second largest in Australia after Lake Eyre North), is surprizingly rarely mentioned, except briefly, in the limnological literature. It is scarcely mentioned, for example, in Hammer's (1986) comprehensive global treatise on salt lakes or the inventory of important South Australian wetlands by Morelli & de Jong (1996).

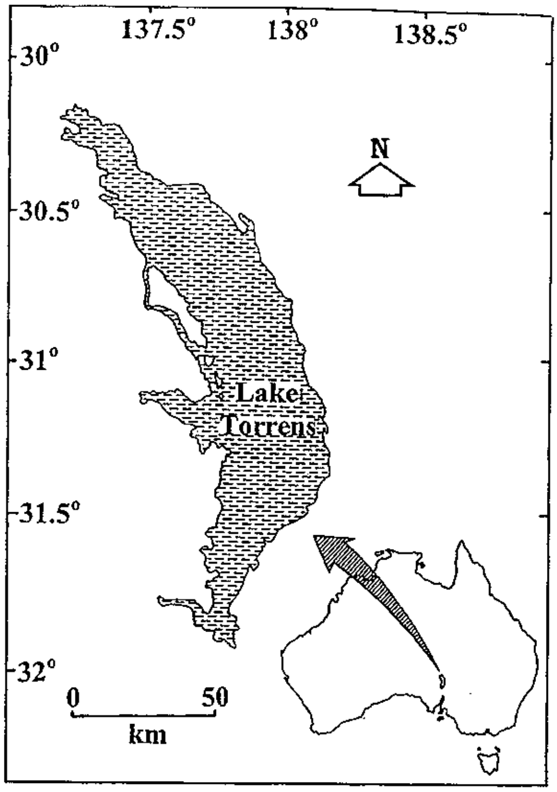

Figure 1. Location of Lake Torrens, Australia.

General limnological features

Lake Torrens is located between 30 and 32° S and 137 and 138° E (Figure 1) and situated at 30–35 m above sea-level. Maximum length is 220 km, and maximum width, ~ 70 km. Total area is 5923 km^2 (upper values of 30 000 km^2 given in some texts, e.g. Gleick (1993), are incorrect; Bowler (1981) gave a surface area of 5640 km^2 and a catchment area of 27 800 km^2). The lake is very shallow; mean depth when full is 0.5 m; maximum depths (1.5 m) occur on the western side of the lake and this part was the last to dry in 1990 as shown by examination of satellite images (Landsat). The volume of the lake when full is ~ 3000 km^3. The bed is not completely flat and areas of low relief (islands in 1989) occur, several associated with mound springs located on the lake bed, especially towards the western margin. These mound springs may be 0.1 to 2 m high as a result of gypsum deposition.

The geology and hydrology has been investigated especially by Johns (1963, 1967) and Schmid (1985, 1990). Bowler (1981) discussed the hydrology of the lake and concluded that under the present climatic regime it would never fill and retain water. The lake is best described as a playa within a graben resting on sediments that are of Cainozoic age and 300 m deep. A geological fault delimits the western edge of the lake which is overlooked by the Arcoona Plateau, a dissected, flat region of sandstone. The eastern edge of the lake lies adjacent to an extensive, low, flat, alluvial plain. The lake arose when the block on the eastern side of the fault or fracture zone sagged at the end of the Cretaceous (~ 70 million years ago) and sediments began to accumulate in the fault-angle valley so formed (Twidale & Campbell, 1993). Gypsum has precipitated in the topmost 100 m of sediments, deposited in Quaternary times, especially towards the lake's centre. Rather small amounts of halite occur on the surface of the lake, a feature explained by Schmid (1990) as due to the low rate of evaporation (50 mm per annum) of groundwater. As a whole, the bed of the lake is gypsiferous clay and large areas remain damp for considerable periods even in the absence of precipitation.

All major inflowing streams arise in the Flinders Ranges to the east of the lake. However, they only rarely discharge into the lake; most debouch their wa-

Table 1. Mean monthly and annual precipitation near Lake Torrens. Data supplied by the South Australian Regional Office of the Bureau of Meteorology and reproduced with permission. Values as mm

Station	J	F	M	A	M	J	Jy	A	S	O	N	D	Ann.
Oakden Hills[1]	14.3	16.4	11.5	12.1	18.6	19.1	12.7	14.3	14.3	15.8	15.2	12.8	177.9
Woomera airport[2]	16.9	21.1	14.9	13.1	23.8	15.0	16.5	14.1	16.1	15.3	17.8	12.7	197.2
Leigh Ck airport[3]	22.7	12.8	33.2	10.7	26.7	17.1	24.4	20.6	12.1	14.6	19.6	39.0	261.7

1 Period of record, 1879–1996
2 Period of record, 1982–1998
3 Period of record, 1949–1998

Table 2. Mean monthly and annual precipitation near Lake Torrens in 1989. Data supplied by the South Australian Regional Office of the Bureau of Meteorology and reproduced with permission. Values as mm. Data for March 1989 in italics

Station	J	F	M	A	M	J	Jy	A	S	O	N	D	Ann.
Oakden Hills[1]	0.0	0.0	*199.8*	55.6	38.2	24.7	26.8	0.0	6.3	7.4	9.8	7.4	367.0
Woomera airport[2]	0.0	0.0	*191.2*	26.0	58.8	27.4	26.2	1.4	1.2	7.2	7.0	9.6	358.0
Leigh Ck airport[3]	0.0	0.4	*175.1*	12.9	32.2	21.8	53.4	0.2	4.2	14.5	64.8	22.6	402.0

ter on to the eastern, permeable plain. Except in 1989, the only water on the lake comprises shallow (< 2 cm deep), isolated, short-lived saline pools which move across the lake under the action of the wind and which result from small episodic rainfall events over the lake itself.

Climate

Mean annual rainfall in the region is ~ 200 mm so that according to most climatic criteria (e.g. Grove, 1977, and Beaumont, 1989) the region is arid. Rainfall events, as usual in such regions, may occur at any time of the year. Table 1 provides data on mean monthly and annual precipitation at three meteorological stations near the lake, two ~ 50 km east of it (Oakden Hills, Woomera airport), and one ~ 50 km to the west (Leigh Creek airport). Maximum air temperatures in summer are frequently > 40 °C (mean maximum, 34 °C) but in winter are often near 1 °C (mean minimum, ~ 4 °C). Mean annual pan evaporation is ~ 3 m.

For lakes in arid regions, it is not mean monthly or annual values of precipitation that are important but rather maximum values of unpredictable events. As indicated, an event of unique magnitude took place near Lake Torrens in 1989. In March of that year, unprecedently high amounts of rain fell over the lake's catchment, with values surpassing any previously or subsequently recorded. Monthly values for the whole of 1989 at Oakden Hills, Woomera airport and Leigh Creek airport are given in Table 2. The most significant rain began to fall on March 9, with peak falls on March 14. The maximum value recorded was 676 mm (Gammon Ranges immediately south of the lake; Robinson & Minton, 1990). Rainfall was unevenly distributed

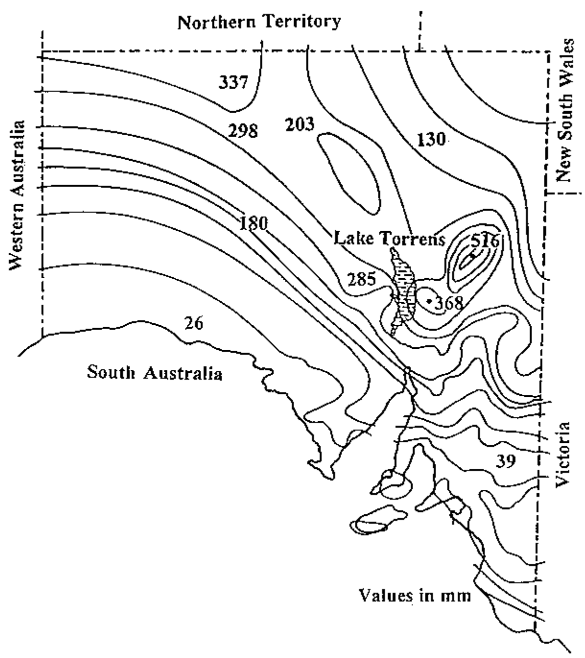

Figure 2. Spatial patterns of rainfall in March 1989. Modified from Robinson & Minton (1990).

Table 3. Major ion composition of interstitial water in Lake Torrens in 1983 and surface water of some water-bodies near Lake Torrens. All data as g l^{-1}

Lake	Na	K	Ca	Mg	Cl	SO_4	$HCO_3 + CO_3$	Salinity
Torrens[1]	103	0.7	0.6	4.3	185	7.0	0.0	301
Eyre South[2]	9.1	0.0	0.6	0.1	14.3	1.3	0.1	25.5
Island Lag.[3]	100	0.3	1.4	4.8	16.0	7.2	<0.1	274
Nr Wirrappa[3]	229	0.1	0.6	2.5	45.3	2.5	0.1	73.9
Nr Ironstone[3]	90	0.6	1.0	10.6	177	9.4	0.2	288
Nr Pernatty[3]	108	0.8	0.7	9.1	189	12.4	<0.1	320

[1] Interstitial brine near centre of lake, 21 May 1983. From Schmid (1985).
[2] From original data summarized in Williams and Kokkinn (1988).
[3] Pool on or near water-body, 3 September 1996. Unpublished data.

Table 4. Salinity of Lake Torrens April 1989 – Feb. 1990. Salinity data as g l^{-1}

Date	No. of samples	No. of sites	Range of salinity	Mean salinity
April 1989	2	2	13–19	16
May	5	4	18–52	29
June	4	3	19–37.5	30
July	1	1	19	19
August	1	1	20	20
September	3	3	22–32	26
October	2	2	30–40	35
December	5	5	31–273	138
January 1990	1	1	181	181
February	1	1	249.5	294.5

as Figure 2 indicates; while some areas received > 500 mm, others towards the coast received < 50 mm.

Overall, it can be seen that the events of 1989 illustrate clearly the central climatic feature so far as the occurrence of episodic lakes in arid regions is concerned: the temporal and spatial uneveness and unpredictability of sufficient rain to form a lake.

Chemical features

The ionic composition of subsurface waters of Lake Torrens was investigated by Schmid (1985). His data relate to near surface interstitial waters collected prior to 1989. No analyses of major ions in surface waters were made in 1989. It is unlikely, however, that the major ionic composition of these differed significantly from that of other surface waters in the region and subsurface brine in the lake itself. A selection of data is provided in Table 3. The table shows that like almost all other inland saline waters in Australia (Hart & McKelvie, 1986), Na and Cl are the dominant ions with only small amounts of HCO_3. For Lake Torrens itself, the pattern of ionic dominance in subsurface water was Na > Mg > K > Ca: Cl > SO_4 > HCO_3, with Na forming 92 per cent (by equivalents) of total cations, and Cl, 97 per cent of total anions. Schmid's (1985) investigations showed some vertical differences in ion proportions; Na and Cl became even more dominant at lower levels.

The pattern of salinity change in the lake in 1989 was determined from surface water samples collected from April to December. Salinity was derived by determination of conductivity and the use of the regression equation of Williams (1986). Samples were diluted when necessary. They were obtained by several collectors at a variety of sites. A summary of results is shown in Table 4. This illustrates the following points:

(i) Despite the large volume of fresh water that entered the lake in March 1989 (~ 3000 km^3), water in the lake was clearly saline by the time first sampled (April 25).

(ii) Spatial variation in salinity occurred, particularly towards the end of 1989. In December, for example, salinities at different sites but collected on the same day (Dec. 21) ranged from 69.3 to > 200 g l^{-1}.

(iii) Notwithstanding the extent of spatial variations, mean lake salinity remained relatively low (< 40 g l^{-1}) for most of the time water was present, i.e. until November. After November, salinity rose rapidly and in early 1990 was at or near > 200 g l^{-1}. It was undoubtedly near saturation shortly before disappearing in early 1990. This pattern is a little different from that found at Lake Eyre South by Williams & Kokkinn (1988) when that lake filled in 1984. Here, salinities were low at first, rose steadily thereafter, and then rapidly during the final months when water was present.

Biological features

Lake inundated

Two elements of the biota were investigated in 1989: the aquatic fauna and the avifauna, particularly the banded stilt (*Cladorhychus leucocephalus*). Only the aquatic fauna is discussed in detail here; the biology of the stilt was investigated by others and has been discussed elsewhere (Phillipps, 1990; Robinson & Minton, 1990) but with details yet to be published. Only a brief synopsis of their results is given.

Aquatic fauna

Samples of the aquatic fauna were obtained at a variety of times between April and December 1989 as opportunities arose. Several collectors were involved, each using slightly different collecting techniques and nets (mostly zooplankton nets). Several sites were involved. Often water samples were not obtained at the time of collection. Despite differences of this sort, a relatively consistent pattern of temporal distribution and taxonomic composition emerged.

The results of the sample analyses are given in Table 5 and Figure 3. Table 5 lists all taxa recorded in 1989 and the range of salinity over which they occurred derived from mean monthly salinities. Figure 3 illustrates the temporal pattern of distribution for all taxa recorded in at least two separate months. Not provided here are estimates made of relative abundances of taxa.

Several obvious points emerge from consideration of Table 5, Figure 3 and the abundance data.

(i). The number of taxa (29) recorded from Lake Torrens is not high but is comparable with the number found in other episodic salt lakes in Australia, namely, Lake Eyre South, the Paroo lakes and Lake Wyara; Williams & Kokkinn (1988), Timms (1993, in press a,b).

(ii). Nektonic and zooplanktonic crustaceans dominated the fauna, with *Parartemia minuta*, *Daphniopsis queenslandensis*, *Moina baylyi* and ostracods the most important. Of the insects, only *Tanytarsus barbitarsis* was recorded abundantly and more than twice, with all other insect groups found only sporadically and always in low numbers.

(iii). Most of the fauna characteristic of predictably-filled salt lakes of South Australia, i.e. those which contain water on an annual predictable basis, was absent, notably calanoid copepods, *Coxiella*, and *Haloniscus searlei*.

(iv). Many of the taxa occurred on an apparently intermittent basis – present on separate occasions but unrecorded between these. Likewise, abundances varied widely. For example, one sample obtained on May 10 was dominated by cladocerans and ostracods with anostracans not abundant (numbers in a subsample were 1000+, 500 and 10 individuals, respectively), whereas a sample obtained later the same month (May 28) was dominated by anostracans with cladocerans and ostracods subdominant (numbers were 1396, 970 and 870, respectively). Shortly afterwards, in a sample obtained on June 4, ostracods dominated with cladocerans and anostracans not important (numbers were 1000+, 4 and 77 individuals, respectively).

(v). Except for *Triops australiensis australiensis*, no well-defined temporal patterns of succession or restriction to particular salinity ranges were obvious. Moreover, salinity tolerance ranges displayed no unusual features for the taxa involved.

A central question which arises from these points is: to what extent is the macrofauna of Lake Torrens similar to that found in other Australian episodic salt lakes and to what extent does it support the hypothesis of Williams & Kokkinn (1988) that most aquatic macroinvertebrates of episodic salt lakes are geographically widespread because such lakes are poor evolutionary loci? Before this question can be adequately addressed, individual taxa found in Lake Torrens (Table 5) require separate comment.

Both species of rotifers found are regarded as cosmopolitan, though until the identity of Australian 'strains' of *Brachionus plicatilis* are discriminated it is appropriate to designate collections of this species from Lake Torrens as *sensu lato*.

The single notostracan recorded, *Triops australiensis australiensis*, is widespread throughout central and northern Australia (Williams & Busby, 1991) where it is usually confined to fresh waters. However, it has been recorded from mildly saline waters by Timms' (1993) in a Paroo lake, viz. at 19 g l^{-1}. Unfortunately, no water sample was collected when specimens were collected. Possibly it was able to survive only during the initial period when the lake

Table 5. Macrofauna recorded in Lake Torrens, 1989, and salinity ranges (derived from mean monthly salinities)

	Taxon	Salinity range (g L^{-1})
Rotifera	*Brachionus plicatilis* Muller	26–30
	Hexarthra fennica (Levander)	29
Notostraca	*Triops australiensis australienses* Spencer and Hall	16
Anostraca	*Parartemia minuta* Geddes	19–30
	Branchinella nov. sp.	19
'Cladocera'	*Daphniopsis queenslandensis* Sergeev	16–30
	Moina baylyi Forro	16–30
	Daphnia sp.	29
Copepoda	*Apocyclops dengizicus* (Lepeschkin)	26
	Metacyclops sp.	16–29
Ostracoda	*Australocypris insularis* (Chapman)	16–35
	Heterocypris nov. sp.	20–35
	Diacypris whitei (Herbst)	29–30
	D. dictyote De Deckker	29–35
	D. compacta (Herbst)	20–(~ 80)
	mytilocypridinid gen. *et* sp. nov.	29
	Platycypris baueri Herbst	29–30
	Trigonocypris subglobosus De Deckker	29–35
	Reticypris walbu De Deckker	35
Insecta	*Necterosoma dispar* (Clark)	26
	Sternopriscus clavus (Clark)	35–138
	Tanytarsus barbitarsis Freeman	26–138
	Tanytarsus sp.	26
	Cladotanytarsus sp.	30
	Procladius paludicola Skuse	35–138
	Pentaneura sp.	26
	Ceratopogonidae	30
	Ephydridae	29
Pisces	*Craterocephalus eyresii* (Steindachner)	26–(138)*

* Dead and dying specimens only.

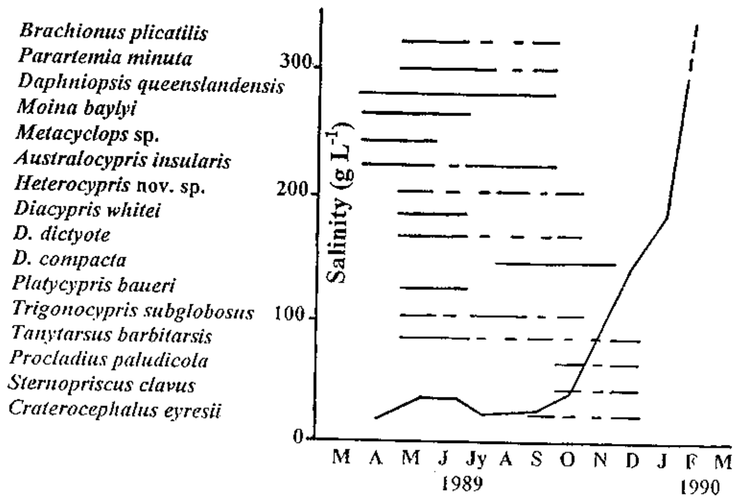

Figure 3. Occurrence of major macrofauna in Lake Torrens in 1989.

contained water after the first inflow of fresh water. It was collected at only one time (April 24) and site.

The anostracans almost entirely comprised *Parartemia minuta*, a species previously recorded from Lake Eyre, Lake Buchanan (Timms, 1987) and some Paroo lakes (Timms, 1993). Specimens of *Branchinella* together with *P. minuta* were also collected on one occasion, a co-occurrence remarkably analogous to that of *B. nichollsi* and *P. minuta* in Lake Buchanan, Queensland, at a salinity of $\sim$ 42 g l^{-1} (M. Geddes, pers. comm.). The species of *Branchinella* at Lake Torrens, however, is not *B. nichollsi* and is considered to be new to science (M. Geddes, pers. comm. 3.8.93).

The two most abundant cladocerans, *Daphniopsis queenslandensis* and *Moina baylyi*, fall within the range of morphological variation for these species. Both probably occur widely in central Australia, having been recorded from Lake Buchanan, the Paroo lakes and Lake Wyara (Timms, 1987, 1993, in press a, b). *Daphniopsis queenslandensis* is also probably the species found by Williams & Kokkinn (1988) in Lake Eyre South, as suggested by them. *Moina baylyi* is similarly widespread; it is known from Western Australia, Lake Eyre, Lake Buchanan, the Paroo lakes and Lake Wyara (Geddes et al., 1981; Williams & Kokkinn, 1988; Timms, 1987, 1993, in press a,b). Given current revisions of species of *Daphnia* in Australia (C. Wilson, pers. comm.) and the emerging complexity of its taxonomy, no specific name can be advanced at present for this taxon with confidence.

Of the copepods, only cyclopoids were collected. The material of *Apocyclops* is close to if not conspecific with *A. dengizicus*, a species found in Western Australia, Lake Buchanan, the Paroo lakes and Lake Wyara (Geddes et al., 1981; Timms, 1987, 1993, in press a, b). No species name could be assigned to the material of *Metacyclops*.

All ostracod species, apart from *Heterocypris* nov.sp., have previously been recorded from Lake Eyre, Lake Buchanan, or elsewhere. Thus, *Australocypris insularis* (=*A. hypersalina*) also occurs in western Victoria, south-eastern South Australia and Western Australia. *Diacypris whitei* has been found in Lake Eyre, Western Australia and elsewhere, *D. dictyote* in south-eastern South Australia, inland NSW and elsewhere, and *D. compacta* from Lake Buchanan to Western Australia. The latter is one of the most ubiquitous hypersaline ostracod species in Australia. The new mytilocypridinid ostracod shares many morphological similarities with *Mytilocypris splendida*, but is larger, has a rounded posterior end and a very broad inner lamella all around the periphery of the shell. It has been recorded from Lake Eyre and many other saline lakes in central Australia. It has also been found in Lake Annean in northern Western Australia. *Platycypris baueri* has been widely recorded from salt lakes in south-eastern and south-western Australian salt lakes. It has not, however, previously been recorded from any in central Australia (including Lakes Eyre, Buchanan, Wyara and the Paroo lakes). *Trigonocypris subglobosus*, on the other hand, is known from all of these lakes. *Reticypris walbu*, originally described from freshwater mound springs north of Lake Torrens, also occurs in Lake Buchanan. It was not found, surprizingly, by Williams & Kokkinn (1988) in Lake Eyre South; they recorded only *R. kurdimurka*. The *Heterocypris* species resembles *H. tatei* redescribed by De Deckker (1979); this also occurs in mound springs north of Lake Torrens. This genus and its Australian representatives display much morphological variation. Possibly it entered Lake Torrens from the Flinders Ranges during the flooding of the creeks there for these creeks frequently have temporary or ephemeral pools. The remains of organisms which live in such waters (e.g. conchostracans) have been found on the dry salt floors of lakes in central Australia.

All insect taxa, so far as can be determined, are widespread forms. *Tanytarsus barbitarsis* occurs not only in southern salt lakes but also in those of central Australia including Lakes Eyre, Buchanan and Wyara.

Craterocephalus eyresii is widespread in central Australia (e.g. Glover & Sim, 1978; Paxton et al., 1989). Curiously, it is absent from some lakes there; it has never been found, for example, in the well-investigated Coongie lakes north-west of Lake Eyre (J. Puckridge, pers. comm.). Although specimens from Lake Torrens were collected on three occasions, only dead and dying specimens were collected in Dec. 1989 and Jan. 1990 (J. Bye, pers. comm.). It has been suggested that populations of this fish in Lake Torrens were derived from small populations known to live in some of the mound springs on or near the lake (J. Read, pers. comm.). In any event, Glover & Sim (1978) have recorded the species at salinities of up to 110 g l^{-1} within the Murray-Darling catchment basin.

It is clear from the above that many of the species recorded in 1989 do indeed appear to belong to a widespread faunal assemblage that seems to characterize central Australian salt lakes of which most if not all are episodic. Characteristic macroinvertebrate species in this assemblage are *P. minuta*, *D. queenslandensis*, *M. baylyi*, *Trigonocypris subglobosus*, *Reticypris walbu* and the new ostracod genus. Additional taxa within this assemblage are cosmopolitan forms (*B. plicatilis*, *H. fennica*) or widespread Australian forms (e.g. *T. barbitarsis*).

It is also clear, however, that differences occur between the faunal assemblages in individual lakes. Thus, although *R. kurdimurka* occurred in Lake Eyre in 1984 (Williams & Kokkinn, 1988), it was not found in Lake Torrens where only its congener occurred, *R. walbu*. *Parartemia minuta* was not found by Timms (in press, b) in Lake Wyara. *Boeckella triarticulata* was not found by Williams & Kokkinn (1988) in Lake Eyre but was found in this lake on an earlier occasion by Bayly (1976) and also occurs in Lake Wyara (Timms, in press, b). Several explanations for these differences can be offered. One, of course, relates to the intensity of collecting: more intensive collecting may have yielded species absent from initial collections. A second one involves subtle differences in the chemistry of the lakes. The ostracods of Lake Torrens, for example, appear to be those tolerant of low calcite saturation levels. A third one involves chance, especially with regard to the occurrence of congeneric species. Chance has already been invoked as an explanation of why similar salt lakes in Western Australia are inhabited by several species of *Parartemia* but only one species in each lake (Williams & Geddes, 1991). Thus, chance may determine which species of *Reticypris*, *R. walbu* or *R. kurdimurka*, reaches an episodic lake first and then excludes its congeners. Chance is also involved in determining the season when episodic rain falls, and this in turn may determine what species occur. Note in this connection that the intermittent salt lakes in southern Australia fill with water first in autumn.

Less easy to explain is the occurrence of two of the unknown species in Lake Torrens (*Branchinella* nov. sp., and *Heterocypris* sp.), particularly since Williams & Kokkinn (1988) hypothesise that episodic salt lakes are not suitable loci for speciation. The occurrence of these new species is anomolous and would seem to negate this hypothesis. However, given that (1) most species in Lake Torrens and other episodic salt lakes in Australia are widespread, (2) studies of Australian episodic salt lakes are still sparse, (3) our knowledge of certain groups remains incomplete (e.g. of *Daphnia*), and (4) small numbers of new and apparently restricted species are recorded whenever an episodic lake is first studied but have subsequently proved on further study to be not restricted to that lake (cf. Williams & Kokkinn, 1988), it is suggested that the hypothesis still remains plausible. Moreover, *Branchinella* and *Heterocypris* are typical of temporary waters and they could have been washed into the lake from temporary pools on the catchment. In the lake they merely survived rather than reproduced. Further studies of episodic salt lakes in Australia are needed, whenever and wherever opportunities arise, as are studies of the distribution of the new species of *Branchinella* and *Heterocypris*. It is suggested that further studies of these species will show they too are widely distributed.

As for the reasons why most species in episodic salt lakes are widespread, these must certainly involve enhanced abilities of resting eggs to survive long dry periods and highly effective dispersal mechanisms. However, the extent, nature and relative importance of these features remains unclear at present.

Avifauna

A large number of bird species was recorded at Lake Torrens during 1989; Bellchambers & Carpenter (1990) listed a total of 64 species, most of which, however, could be regarded as only facultatively associated with the lake. Of waterbirds, the banded stilt (*Cladorhynchus leucocephalus*), silver gull (*Larus novaehollandiae*), gull-billed tern (*Sterna nilotica*) and red-capped avocet (*Recurvirostra novaehollandiae*) were the most important. All bred on the lake in 1989. The breeding of the banded stilt was particularly notable and large populations developed. This species is endemic to Australia and a characteristic bird of salt lakes throughout the continent. Even so, after its original description in 1816, breeding was not recorded until 1930 when it was seen to breed in some episodic salt lakes in Western Australia and South Australia (Lake Callabonna). No further breeding in South Australia was recorded until it bred in Lake Torrens in 1989. The event was closely monitored by a number of ornithologists and popular accounts of their observations were published in 1990 (Phillipps, 1990; Robinson & Minton, 1990). A more detailed account of their observations is in progress. A brief synopsis of their observations was also published in 1996 (Boulton & Williams, 1996).

In brief, breeding began on islands only four weeks after the arrival of water in the lake. Eggs (3–4, sometimes 5) were incubated by both parents continuously for 19–21 days. Newly hatched chicks were not fed by the parents but led immediately to the edge of the lake where they began to feed themselves. Shortly after hatching and beginning to feed, the chicks formed bands with other chicks and some adults and these bands swam away from the nesting sites to new feeding areas. In some cases, the bands moved up to 100 km. Those adults remaining at the nesting sites then began a second breeding cycle. Thus, the first breeding cycle was more or less complete only two months after the filling of the lake, i.e. by early May, and the second cycle by mid-June. Large populations of the banded stilt built up. However, further breeding was restricted by heavy predation of eggs and chicks by the silver gull which had also bred and built up considerable populations. Eventually the breeding of the stilt was terminated by this predation (not by adverse environmental conditions or a shortage of food).

The silver gull is favoured by human waste dumps near most modern Australian townships (Murray & Carrick, 1964) so that large populations of this ubiquitous and omnivorous species have built up over recent decades. Whether these populations now pose a threat to the continued viability of the banded stilt is not known. Even so, for a species like the stilt whose breeding is tied to unpredictable and infrequent events, any threat to its maximum use of resources during these events must *a priori* be considered a potential threat of some importance.

Lake when dry

The attention of limnologists has focussed almost exclusively upon the biota of temporary lakes when these contain water. Nevertheless, information is accumulating which indicates that a smaller, but nonetheless well-defined biota also occurs on the dry bed of at least episodic salt lakes. This typically and mainly comprises scorpions, spiders, ants, beetles and orthopterans. All of these groups have been recorded from Lake Torrens and/or adjacent lakes when dry (P. Hudson, pers. comm.). None occurs in adjacent fully terrestrial areas, that is, all are confined to habitats on the dry surface of Lake Torrens and adjacent lakes. Present evidence suggests that, unlike the aquatic fauna of episodic salt lakes which seems mainly to comprise widespread forms, the 'terrestrial' fauna of episodic salt lakes comprises much more regionally restricted forms. Thus, *Lycosa eyrei*, appears confined to a group of episodic salt lakes in central South Australia (including Lake Torrens and Lake Eyre; Hudson, 1996, 1997). Allozyme electrophoretic studies indicate that gene flow is limited between populations of this (and other) species and reveals that population substructuring is common within the species and often to the finest level of geographical sampling (Hudson & Adams, 1996). The possibility arises, therefore, that the evolution of the 'terrestrial' fauna of episodic salt lakes – including Lake Torrens – shows the reverse of the pattern suggested for their aquatic fauna by Williams & Kokkinn (1988). Extended, this leads to the suggestion that episodic salt lakes are important evolutionary loci for their 'terrestrial' biota, whereas predictably filled salt lakes are not and are populated (if at all) by a widespread fauna. This suggestion remains to be explored. In this connection, it may be noted that the 'terrestrial' fauna of episodic salt lakes has only a limited ability to withstand inundation (days, not weeks).

Acknowledgements

This paper would not have been possible without the cooperation of a large number of people. For collections of water and/or biological samples from the lake, we thank in particular Dr John Bye and colleagues, Flinders University, Mr John Read, Western Mining, Mr Peter Hudson, University of Adelaide, and Dr David Paton, University of Adelaide. For identification of certain fauna we thank the late Mr Robert Taafe (insects), Mr Jim Puckridge, University of Adelaide (fish), and Dr M. C. Geddes, University of Adelaide (anostracans). Mr Hudson, Dr Geddes, Mr Read, Mr Puckridge, Dr Paton, Dr C. Wilson (Australian National University), Dr A. Robinson (Department of Environment and Natural Resources, Adelaide) and Dr Koen Martens (Royal Belgian Institute of Natural Sciences, Brussels) are thanked for information. Mr D. Hart, Department of the Environment and Natural Resources, Adelaide, was helpful in viewing Landsat images and is thanked. The South Australian Office of the Bureau of Meteorology provided climatic information and has allowed its reproduction; this support is acknowledged. Finally, Prof B. V. Timms, University of Newcastle, is thanked for sending a copy at short notice of an unpublished paper.

References

Bayly, I. A. E., 1976. The plankton of Lake Eyre. Aust. J. mar. Freshwat. Res. 27: 661–665.

Beaumont, P., 1989. Environmental Management and Development in Drylands. Routledge, London.

Bellchamber, K. & G. Carpenter, 1990. Birds recorded at Lake Torrens during its 1989 flooding. S. Aust. Ornithologist 31: 1–7.

Boulton, A. J. & W. D. Williams, 1996. Aquatic biota. In M. Davies, C. R. Twidale & M. J. Tyler (eds), Natural History of the Flinders Ranges. Royal Society of South Australia, Adelaide: 102–112.

Bowler, J. M., 1981. Australian salt lakes. A palaeohydrological approach. Hydrobiologia 82: 431–444.

De Deckker, P., 1979. Ostracods from the mound springs area between Strangways and Curdimurka, South Australia. Trans. r. Soc. S. Aust. 103: 155–168.

Geddes, M. C., P. De Deckker, W. D. Williams, D. W. Morton & M. Topping, 1981. On the chemistry and biota of some saline lakes in Western Australia. Hydrobiologia 82: 201–222.

Gleick, P. H. (ed.), 1993. Water in Crisis. A Guide to the World's Fresh Water Resources. Oxford University Press, Oxford.

Glover, C. J. M. & T. C. Sim, 1978. Studies on Central Australian fishes: a progress report. South Aust. Nat. 52: 35–44.

Grove, A. T., 1977. The geography of semi-arid lands. Phil. Trans. r. Soc., Lond. Series B 278: 457–475.

Hammer, U. T., 1986. Saline Lake Ecosystems of the World. Junk, Dordrecht.

Hart, B. T. & I. D. McKelvie, 1986. Chemical limnology in Australia. In P. De Deckker & W. D. Williams (eds), Limnology in Australia. CSIRO and Junk, Melbourne and Dordrecht: 3–31.

Hudson, P., 1996. New records of salt lake lycosids in Australia. Aust. Arachnol. 51: 4–5.

Hudson, P., 1997. Sympatric distribution of an Australian salt lake wolf spider and scorpion. Int. J. Salt Lake Res. 6: 1–3.

Hudson, P. & M. Adams, 1996. Allozyme characterisation of the salt lake spiders (*Lycosa*: Lycosidae: Araneae) of southern Australia: systematic and population genetic implications. Aust. J. Zool. 44: 535–567.

Johns, R. K., 1963. Stratigraphic correlations in the Lake Torrens region. Geol. Surv. S. Aust. Quart. Geol. Notes, 6, April 1963.

Johns, R. K., 1967. Investigation of Lake Torrens and Lake Gairdner. Geol. Surv. S. Aust. Rep. Inv. No. 31. 59 pp.

Meybeck, M., 1995. Global distribution of lakes. In A. Lerman, D. Imboden & J. Gat (eds), Physics and Chemistry of Lakes. Second Edition. Springer, Heidelberg: 1–35.

Morelli, J. & Mark C. de Jong, 1996. South Australia. In R. Blackley, S. Usback & Langford (eds), A Directory of Important Wetlands in Australia. Second Edition. Australian Nature Conservation Agency, Canberra: 435–531.

Murray, M. D. & R. Carrick, 1964. Seasonal movements and habitats of the silver gull, *Larus novaehollandiae* Stephens, in south-eastern Australia. CSIRO Wildlife Res. 9: 160–188.

Paxton, J. R., D. F. Hoese, G. R. Allen & J. E. Hanley, 1989. Pisces. Petromyzontidae to Carangidae. Zoological Catalogue of Australia, vol. 7. Australian Biological Resources Study, Canberra.

Phillipps, H., 1990. The stilt, the shrimp and the scientist. Aust. Nat. Hist. 23: 322–329.

Robinson, T. & C. Minton, 1990. The enigmatic banded stilt. Birds International 1990: 72–85.

Schmid, R. M., 1985. Lake Torrens, South Australia: Sedimentation and hydrology. Ph.D. Thesis, Flinders University, Adelaide.

Schmid, R. M., 1990. Absolute dating of sedimentation on Lake Torrens with spring deposits, South Australia. Hydrobiologia 197: 305–308.

Timms, B. V., 1987. Limnology of Lake Buchanan, a tropical saline lake and associated pools, of North Queensland. Aust. J. mar. Freshwat. Res. 38: 877–884.

Timms, B. V., 1993. Saline lakes of the Paroo, inland New South Wales, Australia. Hydrobiologia 267: 269–289.

Timms, B. V., in press a. Further studies on the saline lakes of the Paroo, inland New South Wales, Australia. Hydrobiologia.

Timms, B. V., in press b. A study of Lake Wyara, an episodically filled saline lake in southwest Queensland, Australia. Int. J. Salt Lake Res.

Twidale, C. R. & E. M. Campbell, 1993. Australian Landforms: Structure, Process and Time. Gleneagles Publishing, Adelaide.

Williams, W. D., 1986. Conductivity and salinity of Australian salt lakes. Aust. J. mar. Freshwat. Res. 37: 177–182.

Williams, W. D., 1990. Salt lakes: The limnology of Lake Eyre. In M. J. Tyler, C. R. Twidale, M. Davies & C. B. Wells (eds), Natural History of the North East Deserts. Royal Society of South Australia, Adelaide: 85–99.

Williams, W. D., in press. Lakes in arid environments. In P. Sullivan & C. Reynolds (eds), The Lakes Handbook, volume 2. Blackwell Science, Oxford.

Williams, W. D. & J. Busby, 1991. The geographical distribution of *Triops australiensis* (Branchiopoda: Notostraca): A biogeoclimatic analysis. Hydrobiologia 212: 235–240.

Williams, W. D. & M. C. Geddes, 1991. Anostracans of Australian salt lakes, with particular reference to a comparison of *Parartemia* and *Artemia*. In R. A. Browne, P. Sorgeloos & C. N. A. Trotman (eds), Artemia Biology. CRC Press, Boca Raton: 351–368.

Williams, W. D. & M. J. Kokkinn, 1988. The biogeographical affinities of the fauna in episodically filled salt lakes: A study of Lake Eyre South, Australia. Hydrobiologia 158: 227–236.